Sexual dimorphism within the stem-group arthropod *Isoxys volucris* from the Sirius Passet Lagerstätte, North Greenland

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Morphometric analyses carried out on 126 specimens of the early Cambrian (Cambrian Series 2, Stage 3) stem-group arthropod *Isoxys volucris* from North Greenland reveal a bimodal distribution, where Morphogroup A is characterised by a significantly wider doublure than Morphogroup B. The dimorphism is interpreted as intraspecific variation related to gender (sexual dimorphism), where the relative numbers of individuals within the two morphogroups are equal (ratio 1:1). The discovery of established sexual dimorphism in *Isoxys* may have implications for the taxonomic discrimination of other stem-group arthropods within the morphologically diverse and disparate animals of the early Cambrian.

Keywords: Sirius Passet Lagerstätte, *Isoxys*, stem-group arthropods, sexual dimorphism, early Cambrian.

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The arthropod *Isoxys volucris* Williams, Siveter & Peel 1996 is the most common fossil in the lower Cambrian Sirius Passet Lagerstätte of Peary Land, North Greenland (Stein *et al.* 2010; Peel & Ineson 2011b) except for the trilobite *Buenellus higginsi* Blaker 1988. The genus is a stem-group arthropod (Legg & Vannier 2013) and is enclosed by an elongate, non-mineralised, bivalved carapace, although it remains unresolved whether it is dorsally folded or hinged (see e.g. Stein *et al.* 2010), and with long antero- and postero-dorsal spines. *Isoxys* has a widespread distribution which is latitudinally restricted to the tropical and subtropical regions (Williams *et al.* 1996; Vannier & Chen 2000). Representatives of the genus have been reported from the lower and middle Cambrian of several countries: Australia (Glaessner 1979; Bengtson *et al.* 1990; García-Bellido *et al.* 2009a); Canada (Walcott 1908; Simonetta & Delle Cave 1975; Conway Morris 1979; García-Bellido *et al.* 2009b; Vannier *et al.* 2009; Kimmig & Pratt 2015); China (e.g. Jiang 1982; Hou 1987; Hou & Bergström 1991; Shu *et al.* 1995; Vannier & Chen 2000; Luo *et al.* 2006; Wang *et al.* 2010, 2012; Fu *et al.* 2011, 2014; Schoenemann & Clarkson 2011; Huang & Wang 2014); France (Vannier *et al.* 2005); Greenland (Conway Morris *et al.* 1987; Williams *et al.* 1996; Peel 2010; Stein *et al.* 2010); Russia (Ivantsov 1990); Spain (Richter & Richter 1927); and U.S.A. (Walcott 1890; Campbell & Kauffman 1969; Briggs *et al.* 2008). *Isoxys volucris* is distinguished from other species of *Isoxys* by, for example, its long, narrow spines and broad, conspicuous, wrinkled doublure. The soft parts of *I. volucris* are rarely preserved and are known only from a few incomplete specimens (Stein *et al.* 2010). This makes comparisons with other species of *Isoxys* difficult and its affinities uncertain, and it has even been surmised that *I. volucris* is not a true member of the genus (Vannier *et al.* 2006, p. 211). However, a cladistic analysis by Legg & Vannier (2013) firmly demonstrated that *Isoxys volucris* belongs to the genus *Isoxys*. Despite having been collected in great numbers, our knowledge of *I. volucris* is fairly limited, partly because only few morphological characters are preserved. However, an elongate, medially placed

structure interpreted as a possible body attachment (Stein *et al*. 2010) occurs sporadically in the studied material. *I. volucris* was described in detail first by Williams *et al*. (1996) and subsequently by Stein *et al*. (2010). The genus *Isoxys* has been interpreted as a pelagic hunter or scavenger (Zhao *et al*. 2014).

Here, we describe morphometric analyses on 126 reasonably well-preserved specimens of *I. volucris* collected *in situ*, which allow a test of recently detected dimorphism in *Isoxys* based on material from China (Fu *et al*. 2014). Furthermore, we examine a number of possible reasons for the observed dimorphism within *Isoxys volucris*.

Geological setting

The fossiliferous beds containing the Sirius Passet Lagerstätte are black slates of the Buen Formation, more specifically the so-called 'Transitional Buen Formation' of Peary Land, North Greenland (Ineson & Peel 2011; Peel & Ineson 2011a, 2011b). It has been correlated with Cambrian Series 2, Stage 3 (Peel & Ineson 2011a), and is roughly contemporaneous with the Chinese Chengjiang Biota. In terms of absolute dating, the age of the formation is about 520–515 Ma (Gradstein *et al*. 2012). During this time interval North Greenland was situated just south of the Equator at approximately 15°S (Fig. 1). The Buen Formation is approximately 210–250 m thick at Navarana Fjord less than 40 km south-west of Sirius Passet (Higgins *et al*. 1991). The Sirius Passet locality is situated in westernmost Peary Land at 82°47.6'N, 42°13.7'W (Fig. 1), close to the eastern shores of J.P. Koch Fjord. The geological setting of the Sirius Passet fossil locality was described in detail by Ineson & Peel (2011) and only a few points need to be added here.

The section is steeply dipping and exposes approximately 12 m of platy, dark grey to black, laminated mudstones belonging to the 'Transitional Buen Formation' (Fig. 2). The section was excavated during the 2011 expedition to the locality. It contains finely laminated mudstones and interbedded intervals of non-laminated to weakly laminated mudstones with weak to moderate degrees of bioturbation; the Lagerstätte is only preserved in the former. Its base and top is covered by scree and thus not exposed. The locality is wedged between the underlying dolostones of the Portfjeld Formation to the east and an intraformational thrust along the western to northern boundary. The majority of the collected fossil material was sampled *in situ* at the main section. In addition, fossils of *Isoxys volucris* have been reported from four other localities in the 'Transitional Buen Formation' in close vicinity to the main outcrop, although these localities have a rather poor fossil yield (Peel & Ineson 2011a). The depositional setting of the Sirius Passet Lagerstätte was

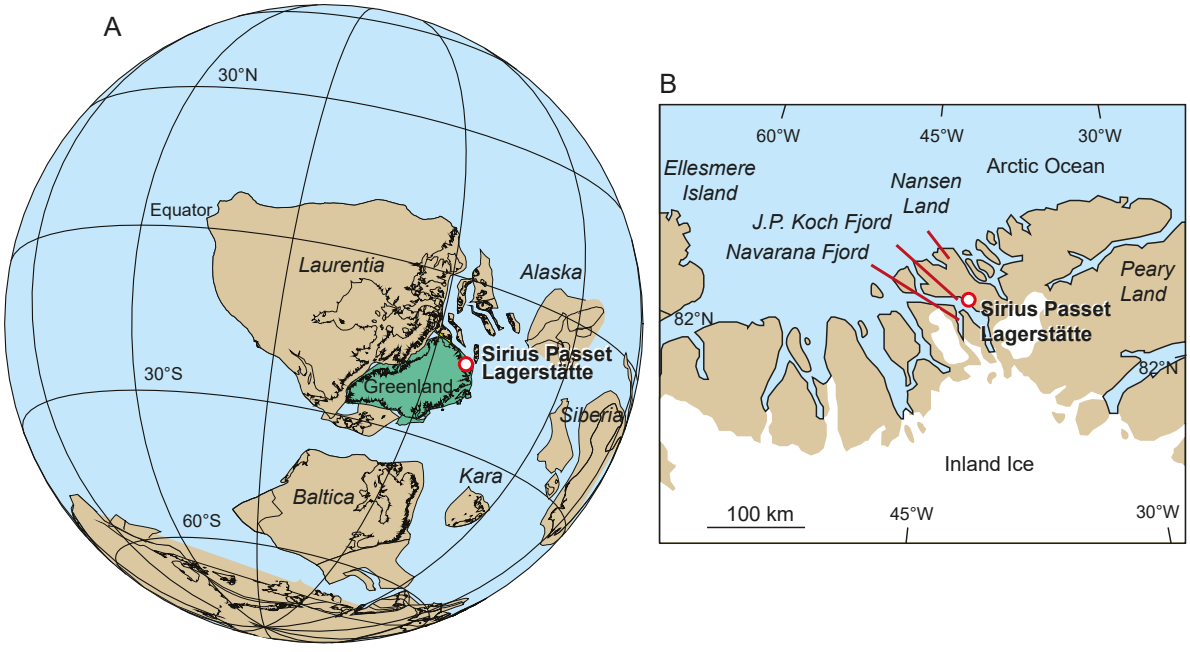

Fig. 1. A: Palaeogeographic map (at 520 Ma) computed by the BugPlates software (Torsvik & Cocks 2009). Greenland, which is marked in green, was part of the Laurentia continent. **B**: Present-day locality map showing the Sirius Passet Lagerstätte situated in westernmost Peary Land near J.P. Koch Fjord.

previously compared to that of the more renowned Burgess Shale Lagerstätte; both are mudstones deposited in relatively deep water adjacent to a carbonate platform escarpment (i.e. the Portfjeld Formation) with low-energy, poorly oxygenated bottom conditions (Ineson & Peel 2011). Periodic interludes of more oxic conditions on the sea bed have been suggested on the basis of intervals of less laminated and more bioturbated mudstones. The fauna is generally believed to be parautochthonous but some fossils appear to have been preserved *in situ* (e.g. Ineson & Peel 2011; Stein *et al*. 2013). The Sirius Passet biota sediments have been interpreted as being deposited in the upper slope coarse-sediment bypass zone (Peel & Ineson 2011b). In a recent study, however, Strang *et al*. (2016) interpreted it as a shelf setting, deposited at or just below the storm wave base, which – based on the occurrence of cyanobacterial activity – was interpreted as being situated in the photic zone.

Material and methods

The majority of the material described herein was collected *in situ* from the main Lagerstätte locality (Locality 1 in Peel & Ineson 2011a) during the 2011 expedition to Sirius Passet led by David Harper. The *Isoxys* specimens were collected within a 3.6 m thick stratigraphic interval. More than 250 specimens of *Isoxys volucris* were evaluated prior to analysis, and 126 specimens were found suitable for an analysis of the doublure. The specimens include both articulated carapaces and single valves (*sensu* Stein *et al.* 2010). All specimens are housed at the Natural History Museum of Denmark, University of Copenhagen, Copenhagen, Denmark (numbers prefixed by MGUH).

Because the internal anatomical characters are very rarely preserved in *I. volucris* (Stein *et al*. 2010), the morphometric analyses have been restricted to characters related to those commonly preserved: total length, total height, doublure width and overall shape of the valve (Fig. 3).

Specimens were coated with ammonium chloride and photographed using a digital DeltaPix InfinityX camera connected to a computer, which allowed images to be processed directly by DeltaPix InSight software. Measurements were made with an inbuilt calibrated scale. The height of a disarticulated valve was measured at the highest distance from the ventral margin to the dorsal hinge line. For open articulated carapaces, height was measured as half the distance between the ventral edge of the right and left valves. The width of the doublure was measured along the same plane as the valve height. The valve length was measured along the hinge line, excluding spines. Both ventrally and dorsally preserved specimens were measured.

Fig. 2. The main locality of the Sirius Passet Biota viewed from the south. Photo J.A. Rasmussen, 2011.

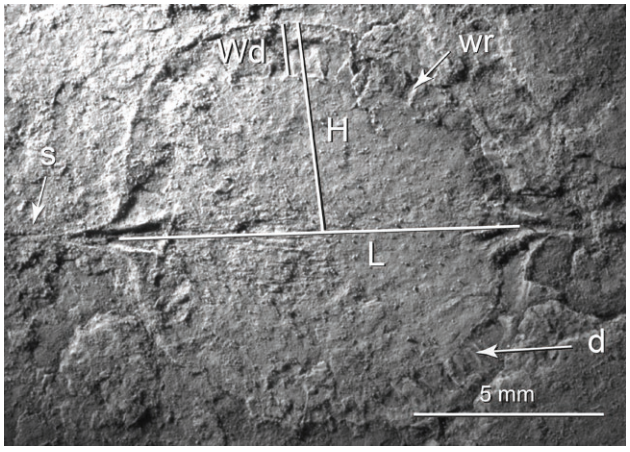

Fig. 3. Slightly oblique view of an open, articulated carapace of *Isoxys volucris* Williams, Siveter & Peel, 1996, showing measured parameters and wrinkles. H = height of carapace measured from the hinge line; L = length of carapace along the hinge line, excluding spines; Wd = doublure width; s = spines; d = doublure; wr = doublure wrinkles.

Mixture analysis

The mixture analysis is a statistical technique to estimate the number of populations that are present within a univariate dataset. It is based on a maximum-likelihood method and also estimates the proportions and parameters of these populations. The technique is useful as it is able to assign the individual specimens to the different populations (Hammer & Harper 2006). This allows the development of hypotheses of affinity for the specimens occurring in areas of overlap and determines the possible boundary between the two morphotypes. Mixture analyses have previously been used to determine sexual dimorphism of fossil organisms when no clear qualitative characters have been available (e.g. Dong 1997; Monchot 1999; Monchot & Léchelle 2002; Fernández & Monchot 2007; Arceredillo *et al.* 2011). Herein, we used the software package PAST v3.14 (Hammer *et al.* 2001) to perform the mixture analysis. PAST calculates the Akaike Information Criterion, AIC, (Akaike 1974) for each hypothesis or model (i.e., the most likely number of possible populations) to resolve the best fit without 'overfitting' the dataset (Hammer & Harper 2006). Thus, the AIC is a measure of the relative quality of the distribution model (unimodal, bimodal etc.), where the preferred model is the one with the lowest AIC value.

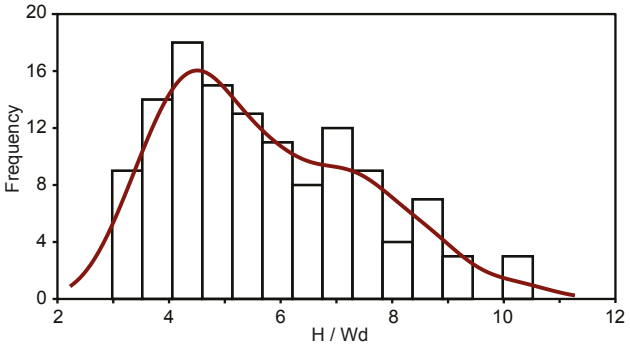

Fig. 4. Histogram showing the frequency of relative doublure width (H/Wd) intervals (14 bins) including the Kernel density line. Notice the two peaks in the distribution.

Results

Mixture analysis was performed on measurements of the relative width of the doublure near the outer rim of the carapace, expressed by the H/Wd ratio. The analysis showed that the lowest AIC value (AIC = 249) appeared when two populations (that is a bimodal distribution) were chosen. For comparison, the AIC value for one population (unimodal distribution) was shown to be 270. For three to six populations, the analysis computed values between 249 and 270. A bimodal distribution appears to fit well with the kernel density shown in Fig. 4 (AIC = 249). The second step was to test if the two populations represent differences in the doublure width of dorsally and ventrally preserved valves. Hence, mixture analyses were performed individually on these groups. The analyses for both dorsal and ventral valves show the lowest AIC value when two groups or populations were selected (dorsal: AIC= 84.4; ventral: AIC = 145.2), and exhibit groupings very similar to those of the collective analysis (Table 1). The similarity of the assigned specimens to the two dorsal groups versus the assignments of the same specimens to the two populations from the collective analysis was 94%. This similarity was 98.7% for the ventral group. This means that there was no significant change in group assignment of specimens when the dorsal and ventral valves were analysed separately, and the analyses detect the same pair of populations, albeit in different frequencies. Altogether, this supports the hypothesis that two morphologically distinct populations of *Isoxys* are present in the Sirius Passet Lagerstätte. The two populations are distinguished as Morphogroup A and Morphogroup B (Table 1; Fig. 5). Morphogroup A represents a population with a relatively broad doublure (low H/Wd ratio; mean = 4.29; std. dev. 0.61) while Morphogroup B represents a population with a relatively narrow doublure (high H/Wd ratio; mean = 7.18; std. dev. 1.25) (Table 2). Morphogroup B shows a greater variation of the H/Wd ratio than morphogroup A. Not surprisingly, the Mann-Whitney test shows that Morphogroup A is significantly different from Morphogroup B with

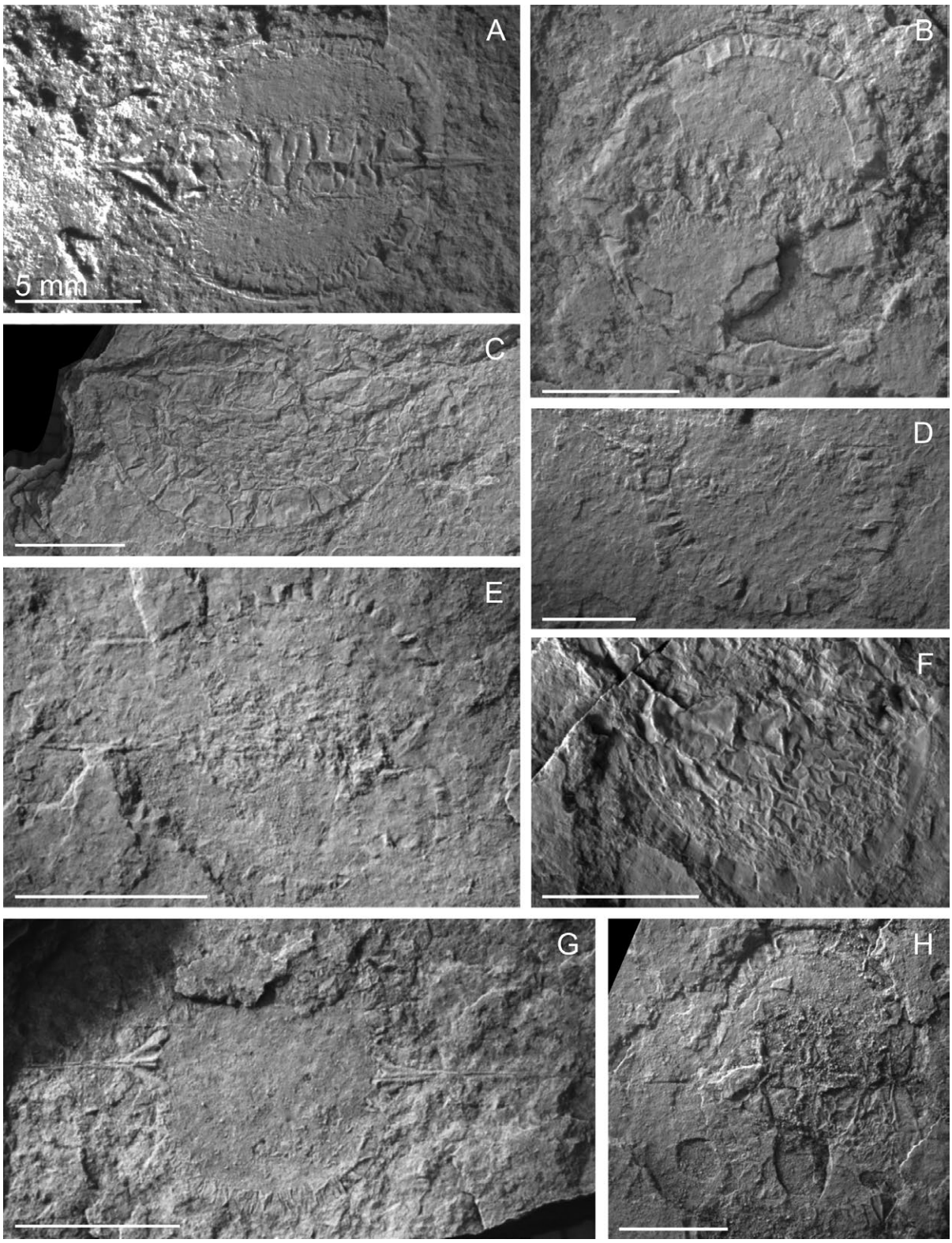

Fig. 5. *Isoxys volucris* Williams, Siveter & Peel 1996. A–D: Morphogroup A; E–H: Morphogroup B; all specimens oriented with anterior to the left. Note the elongate, medially placed possible body attachments in A and B. **A**: MGUH 31624 (175a-180412), dorsal open articulated carapace. **B**: MGUH 31625 (157a-170412), dorsal open articulated carapace. **C**: MGUH 31626 (44a-150312), dorsal valve. **D**: MGUH 31627 (139h-170412), ventral valve. **E**: MGUH 31628 (84j-050412), ventral open articulated carapace. **F**: MGUH 31629 (44f2-150312), dorsal valve. **G**: MGUH 31630 (61c-020412), ventral open articulated carapace. **H**: MGUH 31631 (90a-050412), dorsal open articulated carapace. All scale bars are 5 mm.

regard to the relative width of the doublure (the probability p for the same median is only 3.6×10^{-22}; Table 2). The non-parametric Mann-Whitney test was chosen because of the lack of statistical normality in one of the populations.

A simple XY plot of the total length (L) versus the H/Wd ratio shows clearly that the relative width of the doublure within the two morphogroups is independent of the total size of the animal (Fig. 6). A Student's *t*-test performed on the total length (L) of specimens within each of the two morphogroups indicates that there is no significant difference between the mean values of L (the probability p of having the same mean is 0.19 and thus $p > 0.05$; Table 2).

Table 1. Statistical parameters for morphogroups calculated by mixture analysis on the H/Wd ratio from three independent data sets: Main data (126 specimens), dorsal valves only (50 specimens), and ventral valves only (76 specimens).

Statistical method	Resulting subdivisions	n	Probability	Mean	Stand. deviation	Minimum	Maximum
Mixture analysis	Morphogroup A	63	0.44	4.29	0.61	2.98	5.27
(main data set)	Morphogroup B	63	0.56	7.18	1.25	5.45	10.52
Independ. mixt. analysis	Dorsal group A'	32	0.56	4.00	0.50	3.00	4.90
(dorsal valves only)	Dorsal group B'	18	0.44	6.60	1.40	5.10	10.00
Independ. mixt. analysis	Ventral group A''	29	0.36	4.60	0.50	3.60	5.50
(ventral valves only)	Ventral group B''	47	0.64	7.30	1.20	5.50	10.50

Independent mixture analyses for both the dorsal and ventral specimens are marked as group A' and B', and A'' and B'', respectively. Morphogroup A contains 35 dorsal and 28 ventral specimens; Morphogroup B contains 15 dorsal and 48 ventral specimens. Probability values were calculated for each population by the mixture analyses.

Table 2. Normality test results and univariate statistical data for four selected quantitative parameters related to *Isoxys volucris* morphogroups A and B.

	H/Wd		L /H		L (mm)		Sample level (m)	
	Morphogroup A	Morphogroup B	Morphogroup A	Morphogroup B	Morphogroup A	Morphogroup B	Morphogroup A	Morphogroup B
Normality test								
n	63	63	63	63	63	63	59 (+4 loose sp.)	63
Shapiro-Wilk W	0.97	0.95	0.98	0.96	0.96	0.96	0.93	0.92
p (normal)	0.11	0.01	0.34	0.05	0.05	0.05	0.003	0.001
Univariate statistics								
Mean	4.29	7.18	1.76	1.55	11.27	10.63	3.29	3.38
Stand. deviation	0.61	1.25	0.28	0.25	2.95	2.50	0.58	0.80
Median	4.40	7.10	1.74	1.53	10.98	10.46	3.55	3.58
Minimum	2.98	5.45	1.27	1.06	4.77	6.40	2.05	2.05
Maximum	5.27	10.52	2.40	2.25	16.21	19.56	4.15	5.65
Nonparametric test for equality of medians (Mann-Whitney)								
Mean rank	16.00	47.50	38.58	24.92	33.87	29.63	28.85	32.15
U		0		1125		1717		1721
z		-9.68		-4.19		-1.30		-0.56
p (same median)		3.65×10^{-22}		2.74×10^{-5}		0.19		0.57
Parametric test for equal means (Student's t test)								
Mean			1.76	1.55	11.27	10.63		
Variance			0.08	0.06	8.69	6.24		
t				4.52		-1.31		
p (same mean)				1.41×10^{-5}		0.19		

Relative doublure width, H/Wd; degree of elongation, L/H; total length, L and sample level within the measured section. See Fig. 3 for abbreviations. The lower part of the table shows nonparametric and parametric statistical tests of the equality between the two morphogroups based on the selected characters. All statistical analyses were performed by use of the PAST software package (Hammer *et al.* 2001).

The overall shape of the carapace may be expressed by the ratio between length (L) and height (H), where the relatively longer and more elongate specimens have higher L/H ratios. Morphogroup A (mean = 1.76; std. dev. = 0.28) is significantly different from Morphogroup B (mean = 1.55; std. dev. = 0.25) as shown by the Mann-Whitney test (the probability p for the same mean rank is 2.7×10^{-5}; Table 2), although the two groups partly overlap with regard to L/H (Fig. 7). Thus, Morphogroup A is more elongate than Morphogroup B. The 63 specimens belonging to Morphogroup A include 28 with the ventral surface of the carapace preserved and 35 with the dorsal. Similarly, the 63 specimens of Morphogroup B include 48 ventral and 15 dorsal specimens (Table 1).

It can be added that the two morphogroups regularly occur on the same bedding planes.

There is the possibility that the two morphotypes represent two different, co-existing species. However, it is relatively rare for two near-identical species of the same genus to share the same niche within the same geographic area. In instances where two species of *Isoxys* co-occur in the same unit, the differences tend to be more fundamental. For example, *I. communis* and *I. glaesneri*, which co-occur in the Emu Bay Shale, have markedly different outlines with the former having extended anterior and posterior spines along the hinge area (García-Bellido *et al*. 2009a). Similarly in the Chengjian fauna, *I. auritus* appears to have a bivalved carapace with a dorsal hinge, whereas in *I. curvirostratus* the body is contained within a single shield (Fu *et al*. 2014). *I. curvostriatus* is also more slender with an extended anterior spine (García-Bellido *et al*. 2009a, fig. 2).

Causes for the dimorphism

The character that most clearly distinguishes Morphogroup A from B is the relative width of the doublure expressed by the ratio H/Wd (valve height / width of doublure), but the overall shape of the carapace expressed as the L/H ratio also varies between the two groups, although less significantly. In general, specimens of Morphogroup A have a relatively wider doublure and are more elongate in shape than members of Morphogroup B.

The most common sources of bimodal morphological variation between groups of fossils are differences in ontogeny, taxonomy, gender, habitat, stratigraphy, geographic origin and taphonomy. In this case, we estimate that influence from taphonomy, stratigraphy, habitat and geographic origin are insignificant or absent because all of the studied material was sampled within a homogenous and very limited part of the 'Transitional Buen Formation', more precisely a 3.6 m thick and *c*. 12 m wide section.

Interspecific variation

Because only relatively small morphological differences between the two morphogroups occur (the H/Wd and L/H ratios), and because the relative abundances of the two groups are stable stratigraphically through the measured section (Fig. 8), we regard it most likely that the morphological variation within the group is intraspecific rather than interspecific. In addition, the simultaneous presence of the two morphotypes makes migrational influence unlikely. The Mann-Whitney test (Table 2) revealed that the medians of the two morphogroups show no significant difference with regard to where in the section they were sampled (p = 0.57 and thus p > 0.05 for equality of medians).

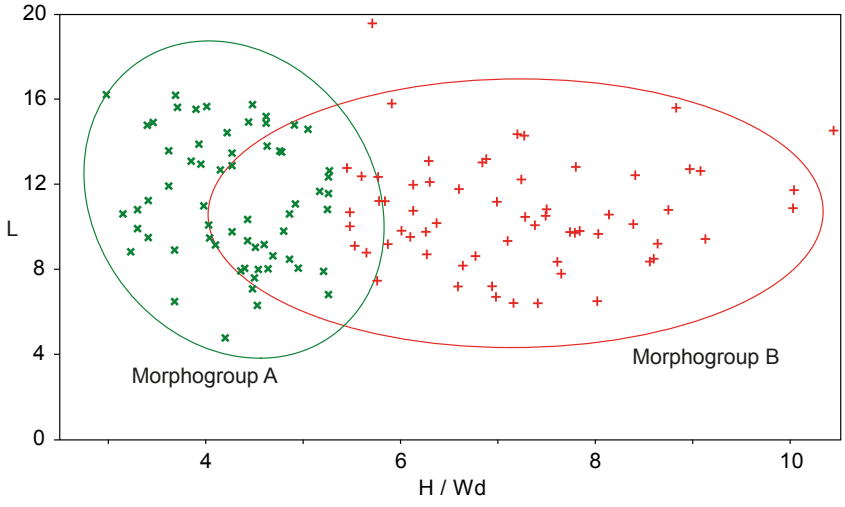

Fig. 6. The relative width of the doublure (H/Wd) plotted against the actual length (L) of the specimen. See Fig. 3 for abbreviations. The two 95% ellipses are indicated. The two morphogroups display a similar distribution of the length (L). The statistical similarity between the two morphogroups with regard to L is further shown by the Mann-Whitney test (Table 2).

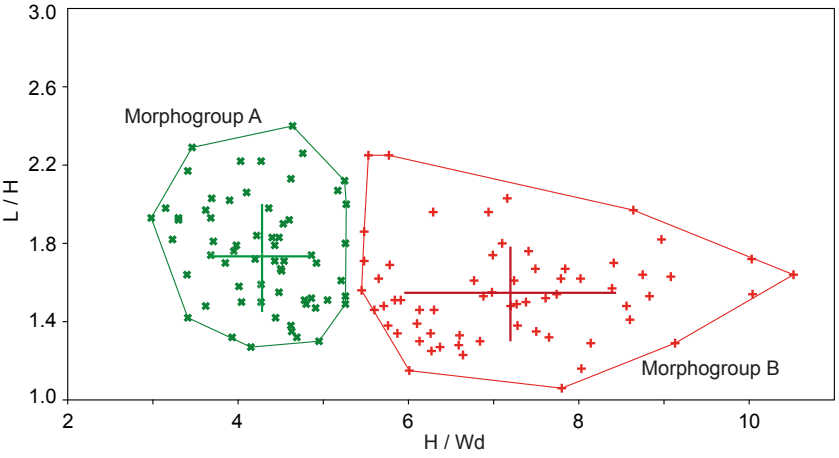

Fig. 7. The relative width of the doublure (H/Wd) plotted against the degree of elongation of the carapace (L/H). See Fig. 3 for abbreviations. The centres of the two crosses indicate the mean values and the crossing lines are the standard deviations of H/Wd and L/H in each morphogroup. The Mann-Whitney test shows that Morphogroup A is significantly different from Morphogroup B with regard to both the H/Wd and the L/H ratios ($p < 0.05$, Table 2).

Ontogenetic differences

A scatterplot showing the relative doublure width (H/Wd) related to the total length (L), demonstrates that the relative width of the doublure is independent of the total length (Fig. 6). This is supported by Student's *t* test, which showed a probability $p = 0.19$ for the same mean length (L) (Table 2). Hence, the distinction in the two morphogroups does not relate to ontogeny.

Sexual dimorphism

Commonly, organisms with presumed male and female morphotypes possess different sexual organs, but these are usually not obvious in fossil material. Moreover, whereas the differences between morphs may suggest sexual dimorphism, it is commonly not possible to recognise females and males and thus the more neutral terms tecnomorph and heteromorph are commonly more applicable. *Isoxys* belongs to the stem-group arthropods (e.g. Legg & Vannier 2013) and accordingly, studies on extant arthropods may provide useful information on possible sexual dimorphism in fossil taxa. For example, extant pelagic arthropods show slight differences in carapace shape with the females having a more elongate outline associated with brood care (Angel 1993).

The concept and recognition of sexual dimorphism has been the focus of research in ammonite populations for nearly a century (see Kennedy 1989 for review). More recently, sexual dimorphism has been documented in several marine euarthropod groups including trilobites (e.g. Cederström *et al*. 2011), naraoiids (Zhang *et al*. 2007), horse-shoe crabs (Smith & Brockmann 2014), ostracods (e.g. Alexander 1932; Schallreuter & Hinz-Schallreuter 2007; Rivera & Oakley 2009) and lobsters (Claverie & Smith 2010). Moreover, dimorphism has been reported from bivalved stem-group arthropods such as *Isoxys auritus* (Fu *et al*. 2014) and the superficially similar *Branchiocaris*? *yunnanensis* (Wu *et al*. 2016). Elsewhere in the arthropod stem, dimorphism has been reported from groups such as the bradoriids (Duan *et al*. 2014). Regarding the recent description of intraspecific, morphological variation within *Isoxys auritus* (Fu *et al*. 2014), it was shown that one morphogroup was characterised by reticulate ornamentation and a relatively wide, marginal doublure, while the other morphogroup showed no ornamentation and a narrower doublure. The two morphogroups of *I. volucris* are distinguished by differences in the relative doublure width and, less significantly, elongation of the carapace, while the doublure is distinctly wrinkled in both morphogroups.

Sexual dimorphism may often result in variances in shape (e.g. trilobites, ostracods and lobsters) or size (e.g. horse-shoe crabs, ostracods and lobsters). In *I. volucris*, the dimorphism is solely related to differences in shape. The differences in shape may be associated with brood care (see above) that has been suggested for the elongate carapaces of *Waptia fieldensis* from the Burgess Shale and may have occurred in other Cambrian arthropods (Caron & Vannier 2016). It is tempting to suggest the more elongate *Isoxys* Morphogroup A comprises the females.

The ratio between female and male individuals in sub-fossil, lacustrine ostracods from Poland was shown to be consistently female-biased, with the percentage of female specimens in each of the six analysed species ranging from 56 % to 77 % (Namiotko & Martins 2008). Similarly, female-dominated ratios were documented within extant Amphipoda (wormshrimps) (Vonk & Nijman 2006) and copepods, where the sex ratio in the latter group may be explained by a late sex change (Gusmão & McKinnon 2009). In comparison, horse-shoe crabs normally display a near 1:1 female/male ratio, but this number may fluctuate tending towards a clearly male-biased ratio under certain circumstances (Mattei *et al*. 2010). The 126 analysed specimens of *Isoxys volucris* were chosen at random purely from a preservational point of view. They split into two equally-sized morphogroups (1:1), and we assume that this ratio represents a reliable estimate of its population structure.

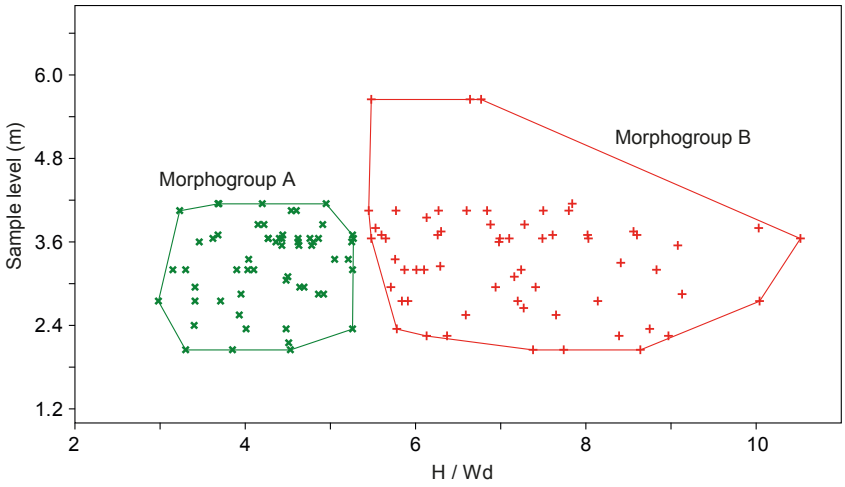

Fig. 8. The distribution of specimens of Morphogroups A and B related to the relative doublure width (H/Wd) and sample level in the measured section. The two morphogroups display a similar distribution in the sampled section, apart from three specimens observed around the 5.7 m level. This is also shown by the Mann-Whitney test, which shows that the two morphogroups have a statistically similar distribution in the sampled section ($p > 0.05$, Table 2).

Ecological differences

We did not observe any sedimentological or palaeontological evidence of fluctuating ecological or environmental conditions through the sampled section, which could be related to the distribution of the two *Isoxys* morphogroups. Therefore, we consider it unlikely that ecological variations influenced the appearance or distribution of two morphogroups of *Isoxys*. This is further supported by their supposed mode of life, which possibly involved a pelagic life style (Williams *et al*. 1996; Vannier & Chen 2000) in open waters (Zhao *et al*. 2014) where they were able to hunt or scavenge as active swimmers, moving up and down in the water column.

Taphonomic differences

Deformation is an obvious source of error when dealing with bivariate ratios. It has been suggested that some tectonic distortion of fossils is indeed present in the Sirius Passet Lagerstätte and may be accountable for the high variation in width/length ratio within the trilobite species *Buenellus higginsi* Blaker 1988 (Babcock & Peel 2007; Arne Thorshøj Nielsen, personal communication 2016). This distortion could potentially explain some of the variation in the bidirectional L/H ratio within *Isoxys volucris*. The specimens were collected from fresh bedding surfaces and were generally randomly oriented, indicating that the shape differences between the morphotypes are not the result of tectonic strain superimposed on a sample of specimens with an already preferred orientation. However, by far the most important character is the relative doublure width shown by the H/Wd ratio. As this is a unidirectional ratio explaining the width of the doublure contra the height of the valve measured along the same plane, it should not be affected by tectonic distortion in any given direction.

Conclusions

A large sample of individuals of the stem-group bivalved arthropod *Isoxys volucris* from the early Cambrian Sirius Passet Lagerstätte contains two morphologically distinct populations. Two morphogroups are recognised statistically, with Morphogroup A having a significantly wider doublure and being on average more elongate in shape than Morphogroup B. Both groups co-exist in roughly equal proportions through the sampled section (ratio 1:1), excluding ecological and environmental (sympatric) and geographic (allopatric) controls on the populations together with migrational events that may have affected the relative proportions of the two morphotypes. This statistical study suggests the existence of sexual dimorphs in some of the earliest animal populations, identifiable on shape parameters. This has implications for unusually speciose early-animal clades, hiding sexual dimorphs during a time of disparity and plasticity in animal evolution.

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